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Interspecies interactions between Microcystis aeruginosa PCC 7806 and Desmodesmus subspicatus SAG 86.81 in a co-cultivation system at various growth phases

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ABSTRACT

In lakes, cyanobacterial blooms are frequently associated with green algae and dominate the phytoplankton community in successive waves. In the present study, the interactions between Microcystis aeruginosa PCC 7806 and Desmodesmus subspicatus were studied to clarify the probable ecological signi cance of algal secondary metabolites; focusing on the role of cyanotoxin 'microcystin-LR' (MC-LR). A dialysis co-cultivation technique was applied where M. aeruginosa was grown inside and D. subspicatus was cultured outside of the dialysis tubing. The concentration of the intra- and extracellular MC-LR and the growth of two species were measured at di erent time points over a period of one month. Additionally, the growth of the two species in the culture ltrate of one another and the e ect of the puri ed MC-LR on the growth of the green alga were studied. The results indicated that the co-existing species could a ect each other depending on the growth phases. Despite the early dominance of D. subspicatus during the logarithmic phase, M. aeruginosa suppressed the growth of the green alga at the stationary phase, which coincided with increased MC production and release. However, the inhibitory e ects of Microcystis might be related to its other extracellular metabolites rather than, or possibly in addition to, MC.

1. Introduction

Monitoring the composition of the phytoplankton populations has shown that algal species undergo a sequence of dominance; a phenomenon called seasonal succession (Reynolds, 1980). According to the seasonal pattern, diatoms (Diatomophyceae) dominate the phytoplankton community during the winter and spring, whereas during the summer green algae (Chlorophyceae) prevail, and in the late summer and autumn cyanobacteria outcompete their predecessors (Sommer, 1989). However, under environmental parameters favouring algal growth such as high nutrient availability (primarily nitrogen and phosphorous) in eutrophic waters, abundant sunlight, warm water temperature (25 °C), and stagnant water, some species of cyanobacteria grow explosively and form large blooms outside of their typical season (Paerl and Otten, 2013; Rastogi et al., 2015; Scholz et al., 2017). Additionally, eutrophication of lakes and climate change in uence the algal seasonal pattern, favouring the formation of harmful cyanobacterial blooms. The occurrence of toxic cyanobacterial blooms, which have undesirable e ects on humans, animals, and aquatic biota, has been reported in many countries throughout the world (Zanchett and Oliveira-Filho, 2013; Svir ev et al., 2017).

Understanding the factors that induce the shift in the phytoplankton composition to the domination of a toxic bloom holds many advantages, especially concerning water quality, treatment, and governance. Recent studies reported that the seasonal uctuation of phytoplankton species is in uenced not only by the environmental factors (Chen et al., 2003; Karad i et al., 2013; Yang et al., 2018) but also by the interspecies interactions (Sukenik et al., 2002; Vardi et al., 2002; Legrand et al., 2003; Leão et al., 2009; Chia et al., 2018). In freshwater ecosystems, cyanobacterial blooms in uence the composition of microbial communities and the co-occurrence patterns of eukaryotic plankton (Xue et al., 2018; L. Liu et al., 2019; M. Liu et al., 2019).

Abbreviations: MCs, Microcystins; MeOH, Methanol; TFA, Tri uoroacetic acid; ACN, Acetonitrile

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Table 1 General characteristics of the controls, fresh embryo transfer (FRESH) and frozen embryo transfer (FET)-derived newborns, and their mothers included in the study. The SD of measures based on international growth references adjusted for gestational age at birth and gender. The mean values ± SD are presented and the significant difference between studied groups for total amount of samples is calculated by Two-Way ANOVA test (P value)

	Country	Control (n = 157)	Fresh embryo transfer (FRESH) (n = 62)	Frozen embryo transfer (FET) (n = 24)	P value
Newborns					
Birth weight (g)	Total	3700 ± 436	3525 ± 548	3805 ± 601	0.02
	FI	3667.7 ± 412.2 (n = 100)	3443.4 ± 502.8 (n = 29)	3846.3 ± 451.4 (n = 18)	
	EE	3758.9 ± 473.9 (n = 57)	3595.8 ± 582.4 (n = 33)	3679.8 ± 970 (n = 6)	
Birth weight SD	Total	0.21 ± 0.8	0.1 ± 1	0.6 ± 1	NS
	FI	0.1 ± 0.9 (n = 100)	0.1 ± 0.9 (n = 29)	0.6 ± 0.9 (n = 18)	
	EE	0.4 ± 0.6 (n = 57)	0.4 ± 1 (n = 33)	0.6 ± 0.9 (n = 6)	
Length (cm)	Total	51.0 ± 1.9	50.3 ± 2.3	51.1 ± 2.3	0.04
	FI	51 ± 2 (n = 100)	50 ± 2 (n = 29)	51 ± 2 (n = 18)	
	EE	51 ± 2 (n = 57)	51 ± 2 (n = 33)	51 ± 4 (n = 6)	
Length SD	Total	0.1 ± 0.8	0.1 ± 0.8	0.1 ± 0.8	NS
	FI	0.2 ± 0.9 (n = 100)	0.3 ± 0.8 (n = 29)	0.0 ± 0.9 (n = 18)	
	EE	0.2 ± 0.8 (n = 57)	0.1 ± 0.7 (n = 33)	0.6 ± 0.5 (n = 6)	
Head circumference (cm)	Total	35.5 ± 1.3 (n = 155)	35.2 ± 1.7	35.4 ± 1.9	NS
	FI	35.5 ± 1 (n = 100)	34.7 ± 2 (n = 29)	35.6 ± 2 (n = 18)	
	EE	35.5 ± 1 (n = 55)	35.5 ± 2 (n = 33)	34.9 ± 2 (n = 6)	
Head circumference SD	Total	0.3 ± 0.8 (n = 155)	0.3 ± 1.1	0.4 ± 1.3	NS
	FI	0.3 ± 0.9 (n = 100)	0.1 ± 1 (n = 29)	0.4 ± 1.4 (n = 18)	
	EE	0.4 ± 0.8 (n = 55)	0.7 ± 1 (n = 33)	0.4 ± 0.7 (n = 6)	
Placenta (g)	Total	565 ± 141	514 ± 118 (n = 61)	642 ± 187	0.04
	FI	626.5 ± 126.4 (n = 100)	578.4 ± 105.8 (n = 29)	687.4 ± 176 (n = 18)	
	EE	456.7 ± 90.5 (n = 57)	454.8 ± 97.9 (n = 32)	504.5 ± 159.6 (n = 6)	
Gestational age (weeks)	Total	40.3 ± 1.2	39.6 ± 1.4	39.8 ± 1.7	0.002
	FI	40.4 ± 1 (n = 100)	39.9 ± 1.3 (n = 29)	40 ± 1 (n = 18)	
	EE	40 ± 1.4 (n = 57)	39.3 ± 1.4 (n = 33)	39.3 ± 3 (n = 6)	
Males	Total	53%	55%	58%	NS
	FI	52%	41%	67%	
	EE	54%	67%	33%	
Females	Total	47%	45%	42%	NS
	FI	48%	59%	33%	
	EE	46%	33%	67%	
Apgar score (5 min)	Total	9 ± 1 (n = 156)	9 ± 1	9 ± 1	NS
	FI	9 ± 1 (n = 100)	9 ± 0.5 (n = 29)	9 ± 0.5 (n = 18)	
	EE	9 ± 1 (n = 56)	9 ± 0.7 (n = 33)	9 ± 0.8 (n = 6)	
Mothers					
Age (years)	Total	31 ± 5	34 ± 5	35 ± 4	< 0.001
	FI	32 ± 5 (n = 100)	35 ± 4 (n = 29)	36 ± 3 (n = 18)	
	EE	29 ± 6 (n = 57)	33 ± 5 (n = 33)	33 ± 5 (n = 6)	

between controls and ART-derived samples in this study ($X^2(3) = 5.52$, $P = 0.138$, chi-square test).

We compared first the genotype-specific methylation levels of placental CTCF6 at H19 ICR and H19 DMR by EpiTYPER to explore potential effects of ART. We did not see any genotype-specific differences between control and ART samples at H19 ICR (Additional file 2: Table S1). At the H19 DMR, we observed increased methylation level in CpG_3 and CpG_16 units in A/A genotype of ART samples (nominal P values: $P = 0.03$ and $P = 0.05$, respectively, Student's t test), but changes were not significant after Bonferroni multiple testing correction.

Genotype-specific DNA methylation at H19 ICR by bisulfite sequencing

We also compared genotype-specific methylation levels of CTCF6 at H19 ICR between control and ART placentas by traditional bisulfite sequencing. To discern maternal and paternal alleles, we used only heterozygous samples (patG/matA and patA/matG). We observed a bias in PCR product: hypomethylated maternal allele of patA/matG genotype was amplified more efficiently compared to hypermethylated paternal allele. Owing to that, we counted the average methylation percentages separately for both alleles and then calculated the total methylation level for each CpG sites (CpG_1-27). We observed similar, but much more prominent common genotype-specific methylation profiles in placenta as we detected by EpiTYPER (Additional file 2: Table S1 and S2).

When comparing genotype-specific DNA methylation within heterozygotes (patG/matA and patA/matG) controls to ART samples, we observed decreased methylation level at sites CpG_1-3, CpG_5, CpG_14, and CpG_24 patA/matG genotype in the ART placentas (nominal P values 0.008, 0.02, 0.001, 0.013, 0.013, and 0.029, respectively, Mann-Whitney) (Fig. 3d). Instead of hypomethylation, we observed increased methylation level at site CpG_26 in patG/matA genotype (nominal P value = 0.041, Mann-Whitney). However, changes in methylation level were not significant after multiple testing correction. We did not see similar trend of decreased methylation

Fig. 3 Genotype- and allele-specific DNA methylation levels at H19 ICR (CTCF6) in control and ART placentas measured by traditional bisulfite sequencing. Methylation levels of selected CpG sites in patG/matA genotype (**a**), paternal allele of patG/matA genotype (**b**), maternal allele of patG/matA genotype (**c**), patA/matG genotype (**d**), paternal allele of patA/matG genotype, and maternal allele of patA/matG genotype. Error bars denote the SD. The numbers of samples are in brackets. Asterisk (*) illustrates nominal P value < 0.05, Mann-Whitney